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DAY AND NIGHT FEEDING HABITAT OF RED KNOTS IN PATAGONIA: PROFITABILITY VERSUS SAFETY?

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Abstract.—By radio-tracking and recording the movements of flocks, the distribution of feeding Red Knots (*Calidris canutus rufa*) was studied day and night at a migration stopover site near San Antonio Oeste, Río Negro, Argentina in March and April 1998. By day, the birds fed in dense flocks of 500–4000 on an area of restinga or rock platform where there were beds of the small mussel *Brachidontes rodriguezi*. By night, this site was deserted, and the birds were found widely scattered over nearby sandflats. It was evident that the birds were feeding at night because variation in the signal strength of the radio-transmitters indicated that the birds were active. Also fresh knot droppings were found in an area which only became exposed by the tide after dark. The reason for the change in feeding distribution may be that the restinga is close to terrestrial habitats that harbor night-adapted predators. Therefore it is avoided at night. By day, it may be safer because better visibility means that predators can be identified more readily. Alternatively, it could be that feeding opportunities become available at night that are better than on the restinga, and this is why the birds feed elsewhere.

ALIMENTACIÓN DIURNA Y NOCTURNA POR PARTE DE *CALIDRIS CANUTUS* EN PATAGONIA: GANANCIA VS. SEGURIDAD?

Sinopsis.—Mediante el uso de radiotransmisores y determinación de movimientos de grupos de individuos de *Calidris canutus rufa* se estudiaron los movimientos diurnos y nocturnos relacionados con la alimentación de esta especie. El trabajo se llevó a cabo de marzo-abril de 1998 cerca de San Antonio Oeste, Rio Negro, Argentina. Durante el día las aves se alimentaron de la almejita *Brachidontes rodriguezi* en una plataforma rocosa en grupos de 500–4000 individuos. Por la noche, las aves se movieron y se díspersaron a unas planicies arenosas que quedaban expuestas al bajar la marea. La señal de los radiotransmisores indicó actividad de movimiento dentro del área en la cual se encontraron heces fecales frescas. La razón de moverse del área rocosa a la planicie para alimentarse durante la noche, pudiera estar relacionada con la presencia de depredadores potenciales nocturnos en la zona rocosa. Por el dia, la zona rocosa pudiera ser un lugar menos peligroso porque las aves muy bien pudieran detectar con mayor facilidad a los depredadores visualmente. Otra alternativa, es que la

planicie de arena pudiera ser un lugar con mayor disponibilidad de alimentos que la zona rocosa y la misma esta disponible durante la noche.

In most parts of the world where Red Knots (*Calidris canutus*) are found outside their breeding season, they feed on bivalves buried in intertidal sediments (Goss-Custard et al. 1977; Piersma et al. 1993; Tulp and de Goeij 1994). Such prey is located by touch rather than by the use of visual cues and swallowed whole (Piersma et al. 1995, 1998). On the coasts of Tierra del Fuego and Patagonia in Argentina, Red Knots (*C. c. rufa*) feed on restingas, broad platforms of rock-like sediment dotted by tidal pools (Murphy 1936). At San Antonio Oeste, Patagonia, the small mussel *Brachidontes rodriguezi* occurs at high densities on the restingas and forms the main prey for migrant Red Knots feeding in daylight (González et al. 1996).

Although González et al. (1996) have shown the importance of the restingas for diurnally foraging Red Knots, there is doubt whether they feed at night on the restingas or feed at night at all. Harrington (1996) states that Red Knots in Tierra del Fuego and Patagonia normally feed only by day, locating their prey by sight, and roost at night. In contrast, González et al. (1996) present data indicating that knots that feed on the restingas by day can only meet their daily food requirement if it is assumed that they also feed at night for much the same period and at much the same intake rates as they do by day. However, attempts to discover whether the birds feed on the restingas at night (by searching for droppings) have shown no evidence that they do (P. M. González, unpubl. data). Thus, the purpose of this study was to establish whether Red Knots that feed on the restingas by day also feed there at night; and if not, to identify where they spend nocturnal low tides and whether they feed there.

STUDY AREA

This study was carried out in the vicinity of San Antonio Oeste, Río Negro Province, Argentina (40°46′S, 65°02′W) where Red Knots occur mainly during northward and southward migration during February–April and September–November. The boundaries of the site (Fig. 1) are the same as that of the Provincial Protected Natural Area ''Bahía de San Antonio'' created in 1993, which is also recognized as an ''International'' site by the Western Hemisphere Shorebird Reserve Network denoting it as a site supporting up to 25% of the flyway population of Red Knots. It includes the study area used by González et al. (1996), the restinga in the vicinity of Los Alamos where there are extensive beds of *Brachidontes*. This has been the main feeding site for Red Knots since studies began in the area in 1989. The site also includes the sandflat known as Banco Reparo where there is another *Brachidontes* bed (Fig. 1).

METHODS

The study was carried out from 5 March–19 April 1998. On 5 March, 321 knots were caught with a cannon-net at a high water roost on Banco

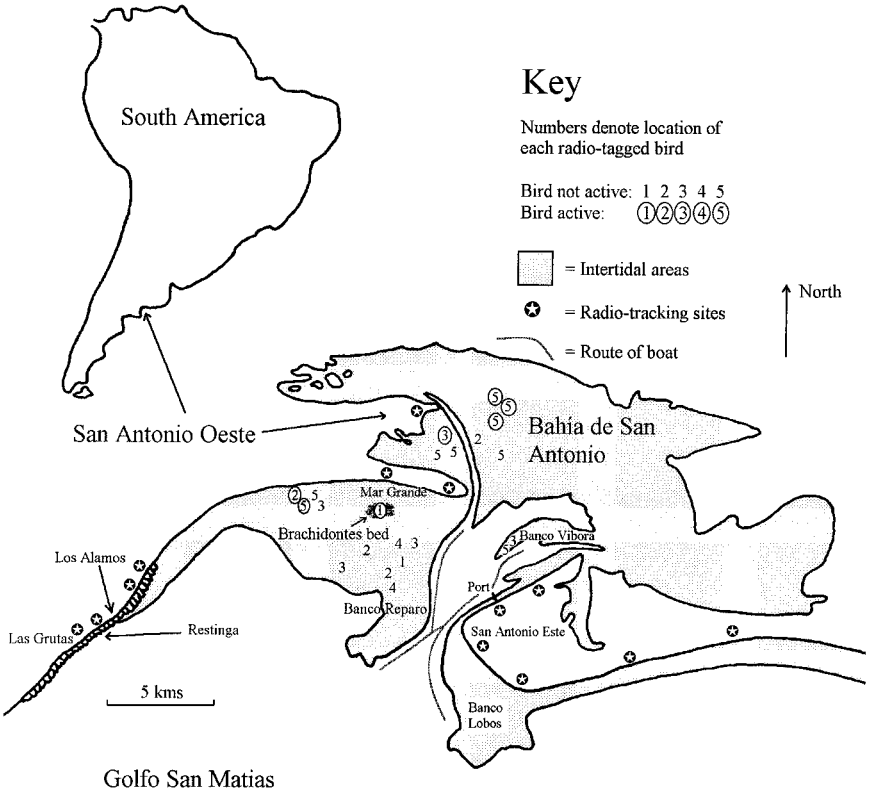

FIGURE 1. The study area at San Antonio Oeste, Río Negro, Argentina: location map and site map detailing places mentioned in the text, radio-tracking sites and the locations at which the radio-tagged birds were found at night (each registration relates to one bird on one night).

Lobos (Fig. 1). From these, five were selected at random and fitted with 1.8 g radio transmitters with a life span of 6 wk (type BD-2G, Holohil Systems, Canada). Radios were glued to clipped feathers and skin on the back (Warnock and Warnock 1993). All five tagged birds were adults (in their third calendar year or older) with a mean weight of 122 g (range 112–134 g). To allow them to recover from any effect of capture, no tracking was carried out until three days after they were tagged. They were tracked from the ground on 14 days and 17 nights between 8 March and 19 April during low tide (±4 h from predicted low water) using a single receiver with Yagi antenna. Apart from Los Alamos, a wide range of sites was visited at night and on the night of 23–24 March, radio-tracking was carried out from a boat (Fig. 1). The maximum range of the radios was 2–3 km. At night, the constancy of the strength of the radio signals was assessed to determine whether the birds were active, and therefore likely to be feeding, (variable signal strength) or inactive/roosting

(constant signal strength). Despite the fact that knots are mainly migrants at San Antonio Oeste, none of the tagged birds left the study area until mid April, like many other Red Knots in the year of study (P. M. González et al., unpubl. data).

To establish whether the knots moved regularly between the restinga where they fed by day and other sites that they might use at night, observations of the movement of flocks were made particularly when low water periods crossed dawn and dusk.

Brachidontes were sampled in our study area to assess availability because knots select only certain size-classes (González et al. 1996). On 23 March, samples of at least 200 mussels were collected at five sites and measured. Two samples were taken from the restinga near Los Alamos, one from the same restinga but 3 km south towards Las Grutas and two from Banco Reparo (Fig. 1). At each site, *Brachidontes* generally occurred in clumps 30–50 cm across. Since there appeared to be a consistent size distribution within each clump with larger mussels towards the middle, each sample was taken as a segment from the middle to the edge of a clump. Within each segment, all mussels of all sizes were measured. No two samples were taken from sites less than 50 m apart.

RESULTS

About 7000 Red Knots were present throughout the study period. During the day, these birds spent most of the time, whether feeding or roosting, in flocks ranging from 500 to 7000 birds.

During 14 diurnal low tides, the radio-tagged birds fed regularly on the restinga near Los Alamos, but none were found there during seven nocturnal low tides (Table 1).

At night, all five birds were located at least twice and four were recorded as active and therefore probably feeding at least once (Fig. 1). On two occasions all five tagged birds were located at the same time at night, both on Banco Reparo (Fig. 1). The first was just before dawn on the night of 14–15 March, the second at dusk on the night of 17–18 March. At all other times, tracking was carried out well after dusk and well before dawn. On these, the birds were only located singly.

Observations around dawn.—On 13 March before dawn, when the restinga was already exposed, none of the radio-tagged birds were located at Los Alamos. Just after dawn, 5000 knots flew from the direction of Banco Reparo, landed at Los Alamos and started to feed. They included all five radio-tagged birds. Similarly, at the same time the following morning, 7000 knots flew from Banco Reparo to feed at Los Alamos. On 15 March, just before dawn all five radio-tagged birds were located on Banco Reparo. They were scattered in different directions. Just after dawn, 1500 knots including Bird 5 were seen feeding on the *Brachidontes* bed on Banco Reparo (Fig. 1). Shortly after, 5000 including the five tagged birds, flew from Banco Reparo to Los Alamos where they fed.

Observations around dusk.—On 10 March, all 7000 knots including the five tagged birds fed on the restinga at Los Alamos throughout the after-

TABLE 1. Record of the radio-tagged Red Knots at Los Alamos, 8 March to 19 April.

Date	Time of low tide	Time of observations	No. of birds present
DAY			
8 March	1410	1120–1705	5
9 March	1518	1330–1630	5
10 March	1624	1500–1846	5
13 March	0633	0900–0920	5
15 March	0745	1045–1150	5
15 March	2001	1600–1645	5
17 March	0843	1030–1246	4
19 March	0947	1035–1135	5
22 March	0553	1010–1020	4
23 March	1309	1410–1600	5
24 March	1414	1110–1130	4
26 March	1624	1245	3
14 April	1958	1525–1605	2
15 April	2028	1610–1725	2
NIGHT			
8–9 March	0248	0015–0100	None
9–10 March	0355	0052–0105	None
12–13 March	0633	0400	None
17–18 March	2101	2300	None
22–23 March	0044	0315	None
23–24 March	0147	0030	None
25–26 March	0356	0130	None

noon. An hour before dusk, while the restinga was still exposed, the whole flock flew off in the direction of Banco Reparo. At dusk on 17 March, all five tagged birds were located on Banco Reparo scattered in different directions. Bird 1 remained there for at least three hours and was active and probably feeding in the vicinity of the *Brachidontes* bed. Close by, in an area that only became exposed by the tide after dark, fresh knot droppings were found containing what appeared to be *Brachidontes* shell. The other four tagged birds disappeared from Banco Reparo soon after dusk and could not be found.

The size distributions of the *Brachidontes* samples from the restinga near Los Alamos and on Banco Reparo show little overlap (Fig. 2). Those on the restinga are almost entirely within the 5–20 mm range found to be taken by Red Knots (González et al. 1996), while on Banco Reparo they are generally larger.

DISCUSSION

Based on our small sample of radio-tagged knots, it appears that diurnal feeding on the restinga at Los Alamos was the norm for our study period, although in other years knots have fed most frequently on Banco Reparo (P. M. González, unpubl. data). The benthic fauna of these areas has not been surveyed and, apart from the *Brachidontes* bed on Banco Reparo,

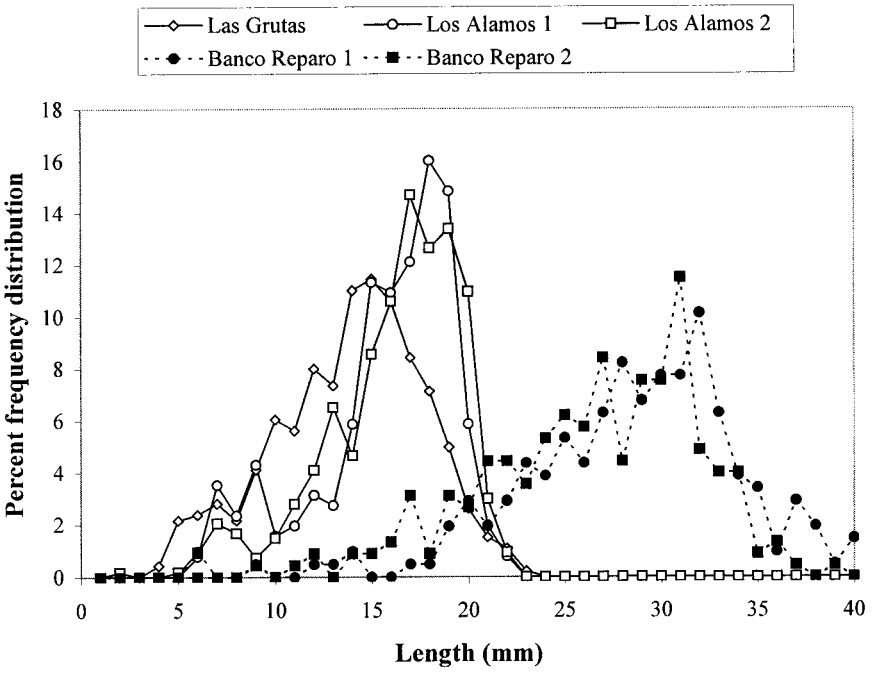

FIGURE 2. Percent frequency distribution of the length of samples of *Brachidontes rodriguezi* occurring on the restinga at Las Grutas (n = 463) and Los Alamos (sample 1, n = 256; sample 2, n = 538) and on Banco Reparo (sample 1, n = 207; sample 2, n = 226).

the only other knot food known to be present is the buried bivalve *Darina* (a staple food of knot elsewhere in Patagonia and in Tierra del Fuego (L. Bala, pers. comm.)). On three days in March 1998, some knots fed briefly by probe-feeding in an area of Banco Lobos where *Darina* was found. Their droppings contained white shell fragments, probably those of *Darina*.

At night, the knots did not feed at Los Alamos, despite the fact that the food available would appear to have been ideal. Instead, they were scattered over the vast expanse of Banco Reparo (about 30 km^2 at low water), in Bahía de San Antonio, on Banco Víbora, and possibly elsewhere.

The fact that all five birds were only found together on Banco Reparo around dusk and dawn suggests that they were then en route between their daytime feeding site on the restinga at Los Alamos and night-time feeding sites in Bahía de San Antonio.

Although little is known about the feeding opportunities that are available in the places where the knots were found at night, there can be no doubt that they did feed in those locations rather than roost. Four of the radio-tagged birds were recorded as active at night and therefore probably

feeding. Moreover fresh droppings containing probable mussel-shells were found at night on the *Brachidontes* bed on Banco Reparo. These results are consistent with the evidence of González et al. (1996), which indicates that the birds must feed at night to fulfill their daily food requirement.

It is curious that knots did not feed on the restinga at night given that suitable sized *Brachidontes* occurred there, and it was frequently used by day. We suggest three hypotheses.

The ''visibility'' hypothesis is that knots cannot see *Brachidontes* in darkness, and so have to feed elsewhere on other prey at night. However, the evidence would appear to be against this. The observation that Bird 1 was found apparently feeding on the *Brachidontes* bed on Banco Reparo and droppings were found containing probable *Brachidontes* shell would indicate that knot are quite capable of finding such prey in darkness (though with what efficiency is unknown). Also, none of the tagged birds were found on the restinga when there was a full moon and this suggests that visibility for locating prey is not the reason why the birds do not feed on the restinga at night.

The ''better opportunity'' hypothesis is that alternative and better feeding opportunities become available at night because of some behavioral change in the prey (Dugan 1981). This hypothesis is suggested by observations that Black-bellied Plovers (*Pluvialis squatarola*) and Dunlins (*C. alpina*) may feed in different places day and night because of changes in the activity patterns and accessibility of their prey. Some prey may become less accessible at night (e.g., *Hydrobia ulvae*); other prey may become more accessible (e.g., *Corophium volutator, Nereis diversicolor* and *N. virens*) (Dugan 1981; Mouritsen 1994). *Brachidontes* are sessile and inactive during tidal exposure both day and night so they cannot be any less accessible to knot at night (except only to such extent as they may be less easy to locate, as discussed above). The fact that some knot were found feeding at night on the poor quality *Brachidontes* bed on Banco Reparo might mean that no feeding opportunity becomes available that is better than the restinga. However, as few birds appeared to feed on the Banco Reparo bed at night, it may not have been an important site. Without more information about the feeding opportunities available at night, this hypothesis must therefore remain a possibility.

The ''predator-avoidance'' hypothesis is that the restinga is close to cliffs, sand dunes and other terrestrial habitats that harbor predators. It is safe to feed there by day because the birds have the advantage of good visibility. It is potentially dangerous to feed there at night so they are risk-sensitive and choose to feed in less rewarding sites far out on the sand flats. This implies that the risk of predation is so high that there is more survival value in avoiding the best feeding site in darkness than in using it (Krebs and Kacelnik 1991).

Probably the most important predators of shorebirds in Patagonia are owls, particularly Great Horned Owls (*Bubo virginianus*) and possibly Short-eared Owls (*Asio flammeus*). Both species are widely distributed in

the region and have been reported as important nocturnal predators of shorebirds elsewhere (Narosky and Yzurieta 1993; Page and Whitacre 1975). One night during April 1998, a Great Horned Owl was observed apparently hunting over Banco Reparo.

Other aspects of the birds' behavior would suggest that predator avoidance is a major influence on their foraging strategy. By day, the knots were watched practically every day feeding on the restinga. They normally fed in dense flocks of 500 to 4000 birds. Peregrine falcons (*Falco peregrinus*) occasionally attacked them and sometimes when this happened they left the restinga. Apart from the benefit of avoiding predators by feeding in flocks, there seemed to be no other reason why they should do this. They could have spread themselves out over the restinga more widely and this would have reduced intraspecific interference (though it may not occur). The tagged birds, or most of them, often fed in the same flock. In contrast to their daytime behavior, at night the tagged birds appeared to be widely dispersed. Even close to dawn and dusk when all five birds were located on Banco Reparo, they were widely spaced. During the middle of the night, no two radio-tagged birds were found together. Two further hypotheses are suggested to explain why the birds fed in flocks by day but were dispersed at night.

The ''predator-mediated distribution'' hypothesis is that it is safer to feed in flocks by day because good visibility and cooperative vigilance aids predator detection (Myers 1984). By night, however, poor visibility means that there is little advantage in numbers so the birds adopt alternative strategies for predator avoidance, as Dunlins do in the Danish Wadden Sea (Mouritsen 1992). By night, flocks might be an attraction to night-adapted predators. Therefore it is safer to disperse.

By day the birds were more concentrated on the restinga than they need have been if distribution of *Brachidontes* were the only factor. It is characteristic of knots that they feed in dense flocks by day, possibly because this behavior affords protection from predators (Goss-Custard 1970). This may arise both from the benefits of cooperative vigilance and from the ability to hide among conspecifics.

The ''food distribution'' hypothesis is that flocking by day and dispersion at night simply reflects the abundance of food on the restinga where they feed by day and the widely dispersed sites where they feed at night. These hypotheses of predator-mediated distribution and food distribution are not mutually exclusive, and both may apply.

High tide roosting behavior was not studied in detail, but a few observations indicate that similar factors may affect choice of roosting sites as affect feeding sites. On three days when high water was in the morning, 3000–5000 knots roosted at Los Alamos. On each previous evening, when the restinga covered before dark, no birds stayed to roost there. The latest departure was 15 minutes after sunset and 30 minutes before it became really dark. Therefore it appears that Los Alamos is avoided at night both as a feeding site and as a roosting site.

Shorebirds appear to avoid roosting close to terrestrial habitats at night

in Roebuck Bay, northwest Australia. There, by day during the austral summer, 80,000 shorebirds of about 20 species (including Red Knot) roost along 8 km of beaches at high tide. These beaches are backed by low cliffs and topped with trees. On nocturnal high tides, the same beaches are deserted (H. P. Sitters, C. D. T. Minton and C. Hassall, unpubl. data). Dunlins at Bolinas Lagoon, California, also change their roosting habitat between day and night (Warnock 1996). By day they roost on open beaches and sand bars. By night they go to a vegetated marsh, presumably because the vegetation hides them from nocturnal predators.

In the same way that the restinga may be avoided at night to escape nocturnal predation, in other places, shorebirds may avoid good feeding habitat by day to escape diurnal predation. For example, in the Chacopata Lagoon, Venezuela, shorebirds use rich feeding sites less frequently by day than by night, apparently to avoid predation by peregrines (Robert et al. 1989; Morrier and McNeil 1991). Similarly, by day, adult redshanks (*Tringa totanus*) choose to feed in less profitable sites in order to avoid predation by sparrowhawks (*Accipiter nisus*; Cresswell 1994).

Taken together, the evidence indicates that Red Knots in particular (and probably shorebirds in general) trade off the benefits (better food or a shorter flight) against the costs (predation) of feeding or roosting in different habitats, a trade-off that may lead them to make different choices by day and by night.

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